

Forceps delivery of a new treefrog species of the genus *Boophis* from eastern Madagascar (Amphibia: Mantellidae)

Denis Vallan^{1,*}, Miguel Vences², Frank Glaw³

Abstract. We describe a new treefrog species of the genus *Boophis* (subgenus *Sahona*) from eastern Madagascar. *Boophis calcaratus* sp. nov. is distinguished from other species of the group by the presence of distinct dermal heel tubercles which are especially well developed in females. We also re-examined the type specimens of *Boophis hillenii*, a species that has not been rediscovered after its description in 1979. According to our analysis this taxon shows no consistent morphological differences to *Boophis idae* and supposed bioacoustic differences may be explained by two distinct call types in this species, and we thus suggest to consider *hillenii* as junior synonym of *idae*.

Keywords: *Boophis calcaratus*, *Boophis hillenii*, *Boophis idae*, new species, *Sahona*.

Introduction

The mainly arboreal genus *Boophis* Tschudi, 1838 currently contains 58 described species (Köhler et al., 2008) and thus represents the largest anuran genus from Madagascar. In their monograph on Malagasy frogs, Blommers-Schlösser and Blanc (1991) distinguished seven phenetic species groups based on morphological criteria, among them the *Boophis tephraeomystax* group with seven species. Since then, *Boophis leucomaculatus* was removed from the genus (Glaw and Vences, 1992), *B. pauliani* was included in the *B. tephraeomystax* group (Glaw and Vences, 1992), *B. granulatus* has changed its name to *B. guibei* (Ohler, 1996), *B. xerophilus* and *B. lichenoides* have been described as new species (Glaw and Vences, 1997; Vallan et al., 1998), *B. difficilis* has been identified as a member of the *B. tephraeomystax* group and synonymized with *B. tephraeomystax* (Glaw et al., 2001), *B. doulioti* has been resurrected (Vences and Glaw,

2002), *B. microtis* has been removed from the genus (Andreone and Nussbaum, 2006), and the subgeneric name *Boophis (Sahona)* has been coined for the *Boophis tephraeomystax* group (Glaw and Vences, 2006).

At present, the subgenus *Sahona* includes the following nine species: *Boophis doulioti* (Angel, 1934), *Boophis guibei* (McCarthy, 1978), *Boophis hillenii* Blommers-Schlösser, 1979, *Boophis idae* (Steindachner, 1867), *Boophis lichenoides* Vallan et al., 1998, *Boophis opisthodon* (Boulenger, 1888), *Boophis pauliani* (Guibé, 1953), *Boophis tephraeomystax* (Duméril, 1853) and *Boophis xerophilus* Glaw and Vences, 1997. In addition, a hitherto undescribed species of the group has been known since long. The aim of the present paper is to describe this new species and to discuss the status of *Boophis hillenii*.

Materials and methods

Animals were searched by means of opportunistic surveys during day and night (using handtorches or headlamps). After anaesthesia with ether or chlorobutanol the specimens were fixed in 90% ethanol and preserved in 70% ethanol. Measurements were taken by D.V. following Duellman (1970), with exceptions as noted below. Specimens examined, their catalogue numbers, sex and locality are summarized in table 1 and the appendix. All measurements were taken with a dial calliper to a precision of 0.1 mm except for snout-vent length, which was measured to the nearest

1 - Natur-Museum Luzern, Kasernenplatz 6, CH-6003 Luzern, Switzerland

2 - Division of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig, Spielmannstr. 8, 38106 Braunschweig, Germany

3 - Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 München, Germany

*Corresponding author; e-mail: Denis.Vallan@lu.ch

Table 1. Measurements (in mm) of *Boophis calcaratus* sp. nov. and type specimens of related taxa in the subgenus *Sahona*.

	Age/sex	Measurements											Proportions				
		SVL	HW	FL	HAL	TL	FOTL	FOL	TD	ED	END	NSD	TD/ED	END/NSD	(TL + FOTL)/SVL	FoL/SVL	HaL/SVL
<i>Boophis calcaratus</i> sp. nov. (holotype) NIMBE 1033824	Adult male	29.5	11.0	5.5	9.5	16.0	21.0	14.0	1.8	4.5	3.1	2.8	0.40	1.11	1.25	0.47	0.32
<i>Boophis calcaratus</i> sp. nov. (paratype) NIMBE 1033825	Adult female	39.5	15.1	8.0	13.0	22.0	28.5	18.0	2.7	5.2	3.8	3.0	0.52	1.27	1.28	0.46	0.33
<i>Boophis calcaratus</i> sp. nov. (paratype) ZSM 5/2009 (originally NIMBE 1033823)	Unknown	33.5	13.2	6.5	10.3	18.0	24.1	14.4	1.9	4.7	3.7	2.4	0.40	1.54	1.26	0.43	0.31
<i>Boophis calcaratus</i> sp. nov. (paratype) NIMBE 1034194	Unknown	27.5	10.5	5.0	8.5	15.0	19.5	11.5	1.8	4.5	2.8	2.2	0.40	1.27	1.25	0.42	0.31
<i>Boophis hilleni</i> (holotype) ZMA 7123A	Adult male	29.5	10.0	6.0	8.5	15.0	21.0	13.5	1.5	4.0	2.1	2.3	0.38	0.91	1.22	0.46	0.29
<i>Boophis hilleni</i> (paratype) ZMA 7123B	Adult male	29.5	10.2	5.5	9.0	16.0	21.0	13.0	1.7	3.8	2.3	2.7	0.45	0.85	1.25	0.44	0.31
<i>Rhacophorus granulosus</i> (holotype) MNHN 1953.160	Unknown	37.0	13.1	9.6	10.1	19.9	27.6	18.0	2.8	4.7	2.9	3.1	0.60	0.94	1.28	0.49	0.27
<i>Hyperolius idae</i> (holotype) NMW 14845	Subadult	17.5	6.7	3.9	5.4	8.2	12.0	6.3	1.1	2.1	1.8	1.1	0.52	1.64	1.15	0.36	0.31
<i>Rhacophorus boulengeri</i> (lectotype) MZUT Am. 90.1	Unknown	33.0	10.9	7.5	10.5	18.2	26.2	17.1	2.8	3.3	3.2	2.8	0.85	1.14	1.35	0.52	0.32
<i>Rhacophorus catalai</i> (holotype) MHNP 1933.237	Unknown	30.0	11.6	5.1	8.2	14.1	19.8	12.4	2.0	4.2	2.6	3.1	0.48	0.84	1.13	0.41	0.27

0.5 mm. The following parameters were measured: snout-vent length (SVL); maximum head width (HW); forearm length (FL); hand length (HAL); tibia length (TL); foot length including tarsus (FOTL); foot length (FOL); horizontal tympanum diameter (TD); horizontal eye diameter (ED); eye-nostril distance (END) and; distance between nostril and snout tip (NSD).

Webbing formulae are given both according to Savage and Heyer (1967) as modified by Myers and Duellman (1982) and Savage and Heyer (1997), as well as according to Blommers-Schlösser (1979).

The following museum abbreviations are used: MNHN = Muséum National d'Histoire Naturelle Paris, MZUT = Museum of Zoology in Torino University, NMBE = Naturhistorisches Museum Bern, NMW = Naturhistorisches Museum Wien, ZMA = Zoologisch Museum Amsterdam, ZSM = Zoologische Staatssammlung München.

Results

Boophis (*Sahona*) *calcaratus* *sp. nov.* (figs 1, 2)

Holotype. NMBE 1033824, adult male, from Ambavaniasy (18°55.647'S, 48°31.397'E, about 800 m above sea level), central eastern Madagascar, collected on 9 March 1995 by D. Vallan.

Paratypes. NMBE 1033825 (adult female), NMBE 1034194 (sex and age unknown), same data as holotype; ZSM 5/2009 (originally NMBE 1033823) (sex and age unknown), from Ambavaniasy (18°57.189'S, 48°30.821'E, about

760 m above sea level), collected on 25 November 1995 by D. Vallan.

Diagnosis. A medium-sized treefrog, assigned to the genus *Boophis* based on its occurrence in Madagascar, the presence of an unforked omosternum (confirmed in NMBE 1033825 by dissection), absence of an outer metatarsal tubercle, and absence of femoral glands. A species of the subgenus *Sahona* based on the lack of webbing between fingers (webbing present in all species groups in the subgenus *Boophis*) and yellowish marbling on the posterior flanks and inguinal region (absent in most *Boophis* species groups). Genetic evidence based on sequences of three mitochondrial genes supports the assignment of the new species to the subgenus *Sahona* (K.C. Wollenberg, personal communication), and its high genetic divergence from the other species in this subgenus (Vieites et al., 2009; as *Boophis* sp. 2). Distinguished from other species of the subgenus by the presence of distinct heel tubercles (absent in all other species except for *B. lichenoides*) and protruding nostrils. Distinguished from *B. lichenoides* by the lack of dermal fringes on arms, legs, and lower lips. Furthermore, distinguished from *B. tephraeomystax* by the presence of a rounded head in dorsal view (vs. slightly pointed). Dis-



Figure 1. Male holotype (NMBE 1033824) of *Boophis calcaratus* in life (dorsolateral view).



Figure 2. Female paratype (NMBE 1033825) of *Boophis calcaratus* in life (dorsolateral view).

tinguished from the other described *Boophis* species with heel tubercles (belonging to the *B. goudoti* group in the subgenus *Boophis*, see Glaw and Vences, 2006): *B. madagascariensis* (Peters, 1874), *B. boehmei* Glaw and Vences, 1992, *B. brachy chir* (Boettger, 1882), *B. reticulatus* Blommers-Schlösser, 1979, *B. rufioculis* Glaw and Vences, 1997, *B. burgeri* Glaw and Vences, 1994, and *B. axelmeyeri* Vences, Andreone and Vieites, 2005 by the absence of hand webbing.

Description of holotype. Body slender; SVL 29.5 mm, for further measurements see table 1; head as long as wide, broader than body; snout round shaped in dorsal view, angular in lateral view; nostrils directed laterally, protuberant; canthus rostralis indistinct, concave; loreal region weakly concave; tympanum distinct, medium sized, rounded, its diameter about 2/5 of eye diameter; moderately distinct supratympanic fold; single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth indistinct; choanae medium-sized, slightly ovoid. Arms slender; subarticular tubercles single; outer and inner metacarpal tubercle not recognizable; fingers without webbing, comparative finger length $1 < 2 < 4 < 3$, first finger thickened without bearing a distinct nup-

tial pad, when fingers 2 and 4 are adressed to each other, terminal finger disks get into contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches between eye and nostril; feet with a small elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well developed; webbing formula: **I** $1^+ - 2$ **II** $1 - 2$ **III** $1 - 2$ **IV** $2 - 1^+$ **V** respectively $1(0.5), 2i(1), 2e(0), 3i(1), 3e(0), 4i(1), 4e(1), 5(0.5)$, lateral metatarsalia separated; comparative toe length $1 < 2 < 3 = 5 < 4$. One distinct dermal tubercle on each heel (diminished in size after preservation in alcohol). Outer foot edge with a series of tubercles which reach to the insertion of the first toe. Skin on the upper surface smooth, throat and chest smooth. Venter slightly granular, thigh ventrally slightly granular, anal region with some tubercles. For measurements see table 1.

Colouration of holotype in life. Dorsally dark brown with many small, sharply delimited darker spots and markings and a transversal dark band between the eyes. Upper surfaces of fore- and hindlegs with distinct dark brown crossbands. Eight crossbands on lower arm and hand (to tip of longest finger), but no crossbands on the upper arm. Small light tubercles on the

shank. Upper and lower lip brown with narrow white crossbands. Iris beige with turquoise periphery. Flanks blackish, especially in the inguinal region, with rounded whitish spots up to several mm in diameter. Venter anteriorly whitish, posteriorly creme. Throat grey, with white spots and markings of different size. Ventral surface of hindlegs dark grey, of feet blackish. There are enlarged whitish tubercles in the cloacal region. Ventral surface of forelegs pinkish, of hands brown.

Colouration of holotype in preservative. After more than ten years in alcohol the colouration is still largely similar to that in life. The brown colour of the back has changed to grey-brown, but is not faded significantly. The iris is grey.

Variation. In comparison to the holotype, the adult female (NMBE 1033825) is larger (SVL 39.5 mm), has larger heel tubercles and a narrower first finger. The dorsal colouration is lighter and the dark dorsal markings are larger. The throat is only slightly darker than the venter, and has no white spots. Measurements of two paratypes are included in table 1. Webbing of the paratypes is similar to the holotype. Morphometric ratios are given in table 1.

Etymology. The species name is an adjective derived from Latin *calcar* (spur). Named after the characteristic spine-like heel tubercles of the new species.

Distribution. The species is known from two localities in central eastern Madagascar (latitudinal range 17°00'–18°55'S, altitudinal range 0–800 m above sea level). NMBE specimens were collected by D.V. at Ambavaniasy. An additional specimen (not collected) of *B. calcaratus* was described and figured in Glaw and Vences (1992) as *Boophis* sp. d and in Glaw and Vences (1994) as *Boophis* sp. c. It had been discovered by F. G. in the southern half of Nosy Boraha, close to Ambodifototra, ca. 17°00'S, 49°51'E, lower than 50 m above sea level. Recently, a photograph taken at Betampona by F. Andreone has been published (Andreone and Randriama-

hazo, 2008) that might also show *B. calcaratus* although the diagnostic heel tubercles are not visible.

Habits. Three specimens from Ambavaniasy were found at night in eucalypt forest at least several meters away from water sitting on branches on leaves between 1.5 and 3 m height. They were observed in syntopy with the following anurans: *Heterixalus madagascariensis*, *H. punctatus*, *H. betsileo*, *Gephyromantis boulengeri*, *Guibemantis tornieri*, *G. liber*, *Boophis madagascariensis* and *B. viridis*. One specimen was found in a strongly degraded forest several meters away from a stream sitting on a branch in 1.5 m height in syntopy with *Platypelis barbouri*, *Mantidactylus opiparis*, *M. lugubris*, *M. femoralis*, *Gephyromantis boulengeri*, *Spinomantis aglavei*, *Boophis madagascariensis*, *B. rappiodes*, *B. luteus* and *B. albilabris*. The specimen from Nosy Boraha was discovered in October 1987 during the day along a small stream that was surrounded by secondary vegetation. The species found in syntopy with *B. calcaratus* are a mixture of pond breeders and stream breeders and do not allow any conclusion about the breeding habitat of *B. calcaratus*. Furthermore, it appears that *B. calcaratus* does not depend on primary forest and therefore might be less affected by deforestation than other *Boophis* species.

Call. Unknown.

Taxonomic status of *Boophis hillenii* and other taxa related to *Boophis idae*

Boophis hillenii was described from Andasibe in 1979, mainly based on supposed call differences to *B. idae* which, however, were not described more in detail or documented by precise data or sonagrams (Blommers-Schlösser, 1979). Surprisingly *B. hillenii* was never unambiguously confirmed despite very intensive amphibian surveys in that region by us and others (e.g., Andreone, 1993). The discovery of *B. calcaratus* in the vicinity of Andasibe led

us therefore consider the possibility that this species might represent the unrecorded *B. hillenii*. However, a closer study of the two male type specimens of *B. hillenii* and comparison with the two available male specimens of *B. calcaratus* revealed that they are not conspecific (for measurements of the holotype and paratype of *B. hillenii*, see table 1). In contrast to *B. calcaratus* there are no heel tubercles in the types of *B. hillenii* and no such tubercles were described by Blommers-Schlösser (1979). In addition the nostrils are more protruding and closer to the snout tip than to the eye in *B. calcaratus* (versus non-protruding and closer to eye in *B. hillenii*, see table 1, but described as of equal distance by Blommers-Schlösser, 1979). The absence of heel tubercles and the non-protruding nostrils in the types of *B. hillenii* and other name-bearing types of similar species and their synonyms (see table 2) are reliable arguments that *B. calcaratus* indeed is a new species and no other available name applies to it. According to Blommers-Schlösser (1979) the tibiotarsal articulation extends to the nostril in *Boophis hillenii* whereas according to our observations (table 1) it reaches between eyes and nostrils. Upon examination, we did not recognize any clear difference between the type specimens of *B. hillenii* and specimens of *Boophis idae* from the Andasibe region. How-

ever, as shown in table 1 in the holotype of *B. idae* (originally described as *Hyperolius idae*) the nostrils are closer to the eye than to the snout tip (vs. equidistant in *B. hillenii*). This could possibly be explained by the fact that the *B. idae* holotype is subadult. In adult *B. idae* the nostrils are equidistant between snout tip and eye (Blommers-Schlösser and Blanc, 1991). The same is true for the hindlimb length. In the holotype of *B. idae* the tibiotarsal articulation does not reach the eye whereas it reaches the eye in adult *B. idae* (Blommers-Schlösser and Blanc, 1991). We therefore propose to consider *Boophis hillenii* as junior synonym of *Boophis idae*. Considering the two very different note types emitted by *Boophis idae* together with its remarkable life-colour variation might explain why Blommers-Schlösser (1979) described *B. hillenii* as a different species despite her otherwise very thorough taxonomical work. Measurements and other morphological characters of primary types of taxa similar to *B. calcaratus* are given in tables 1 and 2. All these taxa – as well as the holotype of *Rhacophorus difformis* Boettger, 1913 (see Glaw et al., 2001) – lack the dermal heel tubercles which are typical for *B. calcaratus*. In addition, *B. calcaratus* differs from the type specimens of *Rhacophorus granulatus* Guibé, 1975, *Hyperolius idae* Steindachner, 1867, and *Rhacophorus catalai*

Table 2. Characteristics of *Boophis calcaratus* sp. nov. and type specimens of related taxa in the subgenus *Sahona*.

Species	Webbing formula	Tibiotarsal articulation reaches...	Tubercle on the heel	Protruding nostrils	Skin of the back
<i>Boophis calcaratus</i> sp. nov. (holotype) NMBE 1033824	1(0), 2i(1), 2e(0), 3i(1), 3e(0), 4i(1), 4e(1), 5(1)	between eye and nostril	present	present	smooth
<i>Boophis hillenii</i> (holotype) ZMA 7123	1(0.5), 2i(1.0), 2e(0.25), 3i(1.0), 3e(0.5), 4i(1.5), 4e(1.75), 5(0.5)	between eye and nostril	absent	absent	smooth
<i>Rhacophorus granulatus</i> (holotype) MNHN 1953.160	1(0), 2i(0.25), 2e(0), 3i(1), 3e(0.25), 4i(1), 4e(1.25), 5(0)	the eye	absent	absent	granular
<i>Hyperolius idae</i> (holotype) NMW 14845	1(1), 2i(1.5), 2e(0.5), 3i(2), 3e(0.5), 4i(1.75), 4e(1.75), 5(1)	not the eye	absent	absent	smooth
<i>Rhacophorus boulengeri</i> (lectotype) MZUT Am. 90.1	1(1), 2i(1.5), 2e(0.5), 3i(2), 3e(0.5), 4i(1.75), 4e(1.75), 5(1)	between eye and nostril	absent	absent	smooth
<i>Rhacophorus catalai</i> (holotype) MNHN 1933.237	1(0.5), 2i(1), 2e(0.25), 3i(1), 3e(0.25), 4i(1.5), 4e(1.5), 5(0.5)	not the eye	absent	absent	smooth

Angel, 1935 (synonym of *B. idae*) by longer hindlimbs, and from *Rhacophorus Boulengeri* Peracca, 1892 (synonym of *B. idae*) by less webbing between the toes. The holotype of *Rhacophorus femoralis* Boulenger, 1882 (synonym of *B. idae*) was not available for this study. However, according to the original description (Boulenger, 1882) the tibiotarsal articulation reaches the center of eye in the holotype of *R. femoralis* (which therefore has shorter hindlimbs than *B. calcaratus*), and heel tubercles are not mentioned.

Discussion

By naming *Boophis calcaratus* and synonymizing *Boophis hillenii* we contribute to clarify the taxonomy in the subgenus *Sahona*. However, the new species is poorly known, and neither its breeding habitat nor advertisement calls are known. Molecular work in progress has confirmed the assignment of this species to the subgenus *Sahona*, but in general, phylogenetic relationships among different lineages of *Boophis* remain poorly resolved. Previous data based on only one mitochondrial gene fragment (Vences et al., 2002) had indicated paraphyly of *Sahona* relative to the subgenus *Boophis* but more recent work (e.g., Glaw and Vences, 2006) grouped species of *Sahona* in a clade. Because all *Sahona* species appear to breed in ponds and species in the subgenus *Boophis* are primarily stream breeders, this aspect of the phylogeny holds interest to understand the evolution of breeding habitat adaptations in mantellids in general. A full taxon sampling of *Sahona*, including *Boophis (Sahona) calcaratus*, and the acquisition of new knowledge on its reproductive ecology, will be crucial to any such study.

We identified substantial morphological differences among specimens herein considered to be conspecific, e.g., between the holotype of *B. idae* and other specimens assigned to this species. We interpret this observation as indicating intraspecific variability, considering that especially regarding hindlimb length (but also

other characters such as adult body size, head proportions and tympanum size) some species of *Boophis* can be rather variable (e.g., Glaw et al., 2001), and other characters can be influenced by the state of preservation of the specimens measured. An alternative explanation would be the existence of further cryptic species in the subgenus *Sahona*. Considering own, unpublished molecular genetic data, it is likely that some species of this subgenus may turn out to be complexes of cryptic species of allopatric distribution, e.g., *Boophis pauliani*. However, although we have identified, in the past years, an enormous number of still undescribed candidate species of Malagasy frogs (Vieites et al., 2009), we have not discovered any morphologically or bioacoustically distinct species in the subgenus *Sahona*, except for *B. xerophilus* and *B. lichenoides*, described already in 1997 and 1998 (Glaw and Vences, 1997; Vallan et al., 1998), and *B. calcaratus*, described herein but already identified as candidate species in 1992 (Glaw and Vences, 1992). This seems to confirm that species diversity in these pond-breeding treefrogs in Madagascar is comparatively low (Vences et al., 2002) and leads us to reject the hypothesis that the available historical specimens and types represent more species of *Sahona* than currently recognized.

Acknowledgements. We are grateful to Franco Andreone (MZUT/MRSN), Alain Dubois and Annemarie Ohler (MNHN), Kurt Grossenbacher (NMBE), and Franz Tiedemann (NMW) for the loan of specimens held in their care, and furthermore to Albertine Razafisoa for the help in the field and to Katharina Wollenberg for sharing unpublished information. The work was carried out in the framework of collaboration accords of the author's institutions with the Département de Biologie Animale, Université d'Antananarivo. We are grateful to the Malagasy authorities, in particular the Ministère de l'Environnement et des Eaux et Forêts, for research and export permits, and to Olga Ramilijaona and Daniel Rakotondravony for their engagement. Funding was provided by Swiss Academy of Sciences (SCNAT) and the Deutscher Akademischer Austauschdienst (DAAD).

References

- Andreone, F. (1993): Kommentierte Liste von Amphibienfunden auf Madagaskar. *Salamandra* **29**: 200-211.
- Andreone, F., Nussbaum, R.A. (2006): A revision of *Mantidactylus microtis* and *M. microtympanum*, and a comparison with other large Madagascan stream frogs (Anura: Mantellidae: Mantellinae). *Zootaxa* **1105**: 49-68.
- Andreone, F., Randriamahazo, H., Eds (2008): Sahonagasy Action Plan. Conservation Strategies for the Amphibians of Madagascar/Stratégies de conservation pour les amphibiens de Madagascar. Museo Regionale di Scienze Naturali, Conservation International, IUCN/SSC Amphibian Specialist Group. Torino, Italy, 95 p.
- Blommers-Schlösser, R.M.A. (1979): Biosystematics of the Malagasy frogs. II. The genus *Boophis* (Rhacophoridae). *Bijdr. Dierk.* **49**: 261-312.
- Blommers-Schlösser, R.M.A., Blanc, C.P. (1991): Amphibiens (première partie). *Faune de Madagascar* **75** (1): 1-379.
- Boulenger, G.A. (1882): Catalogue of the Batrachia Saliensia s. Caudata in the collection of the British Museum. Addenda.
- Duellman, W.E. (1970): The hylid frogs of Middle America. *Monog. Mus. Nat. Hist. Univ. Kansas* **1**: 1-753.
- Glaw, F., Vences, M. (1992): A Fieldguide to the Amphibians and Reptiles of Madagascar. Vences and Glaw Verlags GbR, Köln, 331 S. + 16 colour plates.
- Glaw, F., Vences, M. (1997): New species of the *Boophis tephraeomystax* group (Anura: Ranidae: Rhacophorinae) from arid western Madagascar. *Copeia* **1997**: 572-578.
- Glaw, F., Vences, M. (2006): Phylogeny and genus-level classification of mantellid frogs (Amphibia, Anura). *Org. Divers. Evol.* **6**: 236-253.
- Glaw, F., Vences, M., Andreone, F., Vallan, D. (2001): Revision of the *Boophis majori* group (Amphibia: Mantellidae) from Madagascar, with descriptions of five new species. *Zool. J. Linn. Soc.* **133**: 495-529.
- Köhler, J., Glaw, F., Vences, M. (2008): Two additional treefrogs of the *Boophis ulftunni* species group (Anura: Mantellidae) discovered in rainforests of northern and south-eastern Madagascar. *Zootaxa* **1814**: 37-48.
- Myers, C.W., Duellman, W.E. (1982): A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *Amer. Mus. Novit.* **2752**: 1-32.
- Ohler, A. (1996): Valid name and holotype of the Malagasy frog currently known as *Boophis granulatus* (Guibé, 1975) (Amphibia: Anura). *Copeia* **1996**: 1010-1012.
- Savage, J.M., Heyer, W.R. (1967): Variation and distribution in the tree frog genus *Phyllomedusa* in Costa Rica, Central America. *Beitr. Neotrop. Fauna* **5**: 111-131.
- Savage, J.M., Heyer, W.R. (1997): Digital webbing formulae for anurans: a refinement. *Herpetol. Rev.* **28**: 131.
- Vallan, D., Glaw, F., Andreone, F., Cadle, J.E. (1998): A new treefrog species of the genus *Boophis* (Anura: Ranidae: Rhacophorinae) with dermal fringes from Madagascar. *Amphibia-Reptilia* **19**: 357-368.
- Vences, M., Glaw, F. (2002): Molecular phylogeography of *Boophis tephraeomystax*: a test case for east-west vicariance in Malagasy anurans (Amphibia, Anura, Mantellidae). *Spixiana* **25**: 79-84.
- Vences, M., Andreone, F., Glaw, F., Kosuch, J., Meyer, A., Schaefer, H.-C., Veith, M. (2002): Exploring the potential of life-history key innovation: brook breeding in the radiation of the Malagasy treefrog genus *Boophis*. *Mol. Ecol.* **11**: 1453-1463.
- Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F., Vences, M. (2009): Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proc. Natl. Acad. Sci. USA* **106**: 8267-8272.

Received: January 16, 2009. Accepted: May 28, 2009.

Appendix. Specimens examined

- Boophis calcaratus* sp. nov.: NMBE 1033824 (holotype), Ambavaniasy (18°55.647'S, 48°31.397'E), NMBE 1033825 (paratype), same locality as holotype; NMBE 1034194 (paratype), same locality as holotype; NMBE 1033823 (paratype), Ambavaniasy (18°57.189'S, 48°30.821'E).
- Boophis hillenii* Blommers-Schlösser, 1979: ZMA 7123A (holotype), near Andasibe; ZMA 7123B (paratype), same locality as holotype.
- Rhacophorus granulatus* Guibé, 1975: MNHN 1953.160 (holotype), forest of Moramanga.
- Hyperolius idae* Steindachner, 1867: NMW 14845 (holotype), Madagascar.
- Rhacophorus boulengeri* Peracca, 1892: MZUT Am. 90.1 (lectotype), Andrangoloaka.
- Rhacophorus catalai* Angel, 1935: MHNP 1933.237 (holotype), surroundings of Fianarantsoa.